

THE REPRODUCTIVE CYCLES OF THREE VIVIPAROUS TELEOSTS, ALLOOPHORUS ROBUSTUS, GOODEA LUITPOLDII AND NEOOPHORUS DIAZI¹

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Extensive taxonomic and descriptive work has been done on the Goodeidae, a family of fresh-water viviparous cyprinodonts from Mexico, but very little is known about their reproductive cycles. Except for a detailed three-year laboratory study on *Neotoca bilineata* (Mendoza, 1939), no other major study on the reproductive cycles of the goodeids has been made either in the laboratory or in the field. The only other principal source of information on the breeding cycles in the family is in Meek (1904), in which a brief and inadequate statement is included in the taxonomic description of each species. Miscellaneous information on the reproductive cycles of the goodeids also is scattered in many of Turner's articles but he made no detailed study of any one species.

Because of the scarcity of this information, it was proposed to make an analysis, from field specimens, of the female reproductive cycles of three species in the family. This study concerns the duration of the female cycle, the number and size of broods, the length of the gestation period, etc. This is the first intensive study that has been made of the reproductive cycles from specimens collected in their natural habitat.

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MATERIALS AND METHODS

This study concerns three members of the family Goodeidae: Alloophorus robustus (Bean), Goodea luitpoldii (Therese von Bayern and Steindachner), and Neoophorus diazi (Meek). The three species were collected from Lake Pátzcuaro. They were chosen because they inhabit the same lake and because it was possible to get a continuous supply of adults throughout the year.

Mature Alloophorus and Goodea females normally range from 90–110 mm. in length, although exceptionally large specimens of each species may exceed 130 mm. Mature females of *Neoophorus* range from 70–90 mm. in length.

The writer relied entirely on local fishermen for aid in collecting specimens. Because of the exuberant growth of reeds, lilies and other vegetation near the shore, the local fishermen use the much-publicized "butterfly" nets as scoops and work from their small canoes in groups of three to five. In the open lake the fishermen use large seines that measure 300 feet or more in length.

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This study is based on a total of 3261 females collected during 1957; approximately 50 females of each species were collected twice each month throughout the year. Specimens were divided as follows: 1010 *Alloophorus*, 1117 *Goodea* and 1134 *Neoophorus*. Similar collections, numbering more than 6000 females, were made during 1956 and 1958 but these were used for reference and comparison purposes only. The average size of all collections was 47 ovaries. Some females were collected alive in the lake and others were purchased in the local market since fresh fish were available at least once per week. The fishermen normally bring in only mature adults; they show no preference for either sex or stage of gestation. *Alloophorus* and *Neoophorus* normally are collected along the shore of the lake; *Goodea* usually is collected in open water but may prefer the shore during the breeding season. Lastly, in obtaining specimens in the market, a definite effort was made not to select only large gravid specimens but to take all females, regardless of size or stage of gestation.

In these viviparous species, the ovary is a single structure, compact, spindleshaped, hollow, and continuous caudad with the oviduct which in turn opens to the outside at the genital pore. The ovary has ovigerous tissue but it also acts as a uterus, for all development from fertilization to birth occurs in the ovarian lumen. When the young are ready for birth, they escape from the sacculated ovary and emerge as free-swimming forms.

Upon collection, each ovary was removed and preserved either in formalin or special fixatives such as Bouin's or Zenker's fluids. All ovaries collected were preserved, regardless of the stage of gestation, and placed in one of the following categories : immature ovaries, resting ovaries, ovaries with growing eggs, ovaries with free eggs, ovaries with embryos in different stages of development, and post-partum ovaries. On classifying the gonads into different stages, relatively little difficulty was encountered. Ovaries without free eggs or young were dehydrated and cleared in cedarwood oil. The gonads then were examined with a stereoscopic microscope and classified into the proper stage. Ovaries with embryos in actual stages of development were placed into one of twelve classes according to size. The smallest group ranged from 3.5-5.0 mm. in length and successive groups or classes were formed at increments of 2.5 mm. (*e.g.* 5.1–7.5 mm., 7.6–10.0 mm., etc.); the largest group was 30.1-32.5 mm. (in *Goodca*).

Stages of Gestation

The data on the three species are given concurrently, that is, comparable stages of development are considered at one time for all three forms. The principal description is based on *Alloophorus* and is followed in turn by the ones on *Goodea* and *Neoophorus*.

Immature ovaries

Immature ovaries in all three species measured from 1–2 mm. in maximum width by 15–20 mm. in length. The typically immature ovary has delicate external walls and internal folds; eggs vary up to 350 μ and are densely packed in the anterior half or two-thirds of the gonad. Measurement of the diameter of the small ovaries was made with a micrometer eyepiece in a stereoscopic microscope; the length and diameter of the larger ovaries were measured with a millimeter ruler.

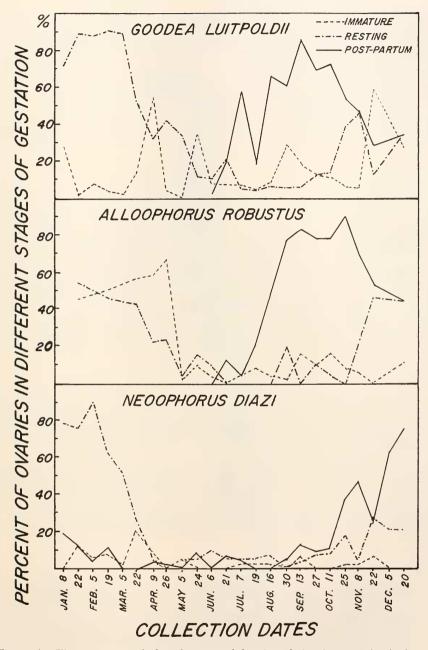


FIGURE 1. The occurrence during the year of females of the three species in immature, resting and post-partum stages. The number of ovaries in different stages appears as percentage figures of the day's collection.

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Normally, few immature females were collected. Figure 1 shows that from January to April the number of these ovaries in *Alloophorus* is high, between 54.8 and 67.3% of the individual collections; thereafter the number drops markedly and remains low during the rest of the year. After spring very few immature females were captured. Figure 1 indicates that in *Goodca* immature ovaries did not follow quite the same pattern of appearance as those of *Alloophorus*. In *Neoophorus*, on the other hand, immature females appeared uniformly throughout the year, usually forming 10% or less of the collections. At no time were immature ovaries in this species as abundant nor did they have the pre-season high so clearly evident in *Alloophorus*.

Resting ovaries

Resting ovaries are mature but do not contain young. These ovaries vary from 2–3 mm, in diameter and up to 20 mm, in length in *Ncoophorus* and 20–30 mm, in length in *Goodea* and *Alloophorus*. The external wall and internal folds are very thick. Eggs are few in number and vary in size but do not exceed 350 μ .

In all three species, the number of females in a resting condition is high during early spring but drops abruptly during early May in *Alloophorus* and *Goodea* and during early April in *Neoophorus* (see Figure 1). In general the number of resting ovaries decreases as the breeding activities start; thereafter the resting ovaries constitute a small but variable percentage of the collections until late summer, at which time breeding ceases. During winter the number of resting ovaries again rises and reaches a peak in the early spring, at which time breeding is resumed.

Ovaries with growing eggs

Ovaries in this condition resembled resting ovaries but differed in that eggs exceeded 350μ and had grown to a maximum of 1 mm. in *Goodea* and *Alloophorus* and approximately .5 mm. in *Neoophorus*. All eggs in this category were still enclosed in a follicle embedded in the ovarian tissues. Measurement of the eggs was made with a micrometer eyepiece.

Growing eggs generally appeared during January and February although the precise time of appearance varied between the three species. If the sampling was representative, *Goodea* had a slightly longer period of egg growth than *Alloophorus*. Growth of new eggs stopped during June in both species and was not seen in later collections. Growth of eggs in *Neoophorus*, however, started at the same time but continued until the end of October.

Ovaries with free eggs

All ovaries with free eggs in the ovarian lumen, regardless of stage of development, were arbitrarily placed in this category. The eggs varied from stages near time of fertilization to stages with young approximately 3 mm. long. Such young were still enclosed within the egg membranes and were coiled around the yolk-like mass. At about this time (3 mm.) the young escape from the membranes and straighten out.

In Goodea and Alloophorus, ovaries with free eggs appeared in collections during April, May and June, a period of 2 to 2.5 months; thereafter, free eggs never appeared in the collections. In Neoophorus, ovaries with free eggs first appeared

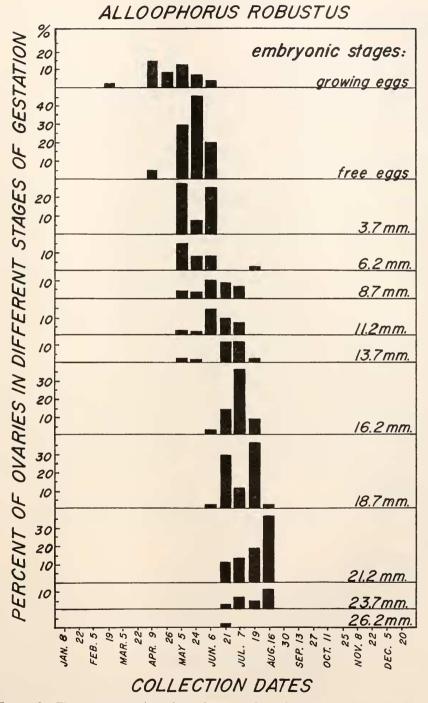


FIGURE 2. The appearance throughout the year of ovaries of *Alloophorus robustus* with embryos in different stages of development. For any one day, the bars represent the percentage of ovaries in each stage of gestation.

during February and thereafter were present continuously until November, at which time they disappeared.

Ovaries with young 3.5 to 32.5 mm. long

In all ovaries with measureable young the following procedures were employed. The diameter and length of each ovary were determined with a millimeter ruler. Following the measurement of the ovary, all young in each gonad were removed and thoroughly mixed in a petri dish. Four specimens then were chosen at random and measured with a ruler from the tip of the snout to the posterior edge of the caudal fin. The average of the four figures was derived and recorded as the size of the young in that particular ovary.

Development of the young was similar in both *Alloophorus* and *Goodea*. Embryos in the 3.5–5-mm. class appeared either in late April or early May. From this time on, developing young were found throughout the breeding season; reproduction ceased after August. While cessation was abrupt in *Alloophorus*, there were scattered females of *Goodea* that were late in their cycle as compared to the bulk of the population. For example, while most young of *Goodea* had reached a size of 23.7 mm. by the middle of July, one female was found on December 20 with young 23.7 mm. long. Figure 3 shows this and other similar examples. Most young of *Alloophorus* were born after they reached 21.2 mm. although some reached 26.2 mm. before birth. In *Goodea*, however, many young exceeded 21.2 mm.; some even reached a maximum of 31.2 mm. before birth. There is a noticeable temporal delay in the appearance of the larger sizes, that is, the larger the class size, the later the appearance of the embryos in the collections.

In *Neoophorus*, the reproductive period extended over eight or nine months. Embryos first appeared during the latter part of March and thereafter appeared continuously until January or February of the following year, at which time reproduction was suspended for a brief period of one or two months. Figure 4 shows embryos of maximum size were still present on December 20, 1957, the last collection of the year. Collections made during 1958 indicate that the 1957 breeding cycle did not terminate until February of 1958. It is similarly noted that one gravid female appeared in January 1, 1957; this female no doubt represents the end of the 1956 breeding season.

The collections of the three species made during the years of 1956 and 1958 strongly support the characteristics of the reproductive cycles as expressed during 1957.

Post-partum ovaries

This category identifies all ovaries from which young have recently been expelled. Immediately after the birth of young these ovaries appeared thin-walled and flaccid, the internal folds were thick and swollen and there were few eggs visible. Later, the ovarian tissues underwent regression but the ovary generally remained thick. Still later, the gonads again resumed the characteristics of a resting condition.

In *Alloophorus* the post-partum ovaries appeared on June 21 and thereafter appeared in large numbers in all collections until the end of the year (see Figure 1). After October 25 the number of these ovaries dropped, concomitant with the rise in the number of resting ovaries. At this transitional point it because more difficult

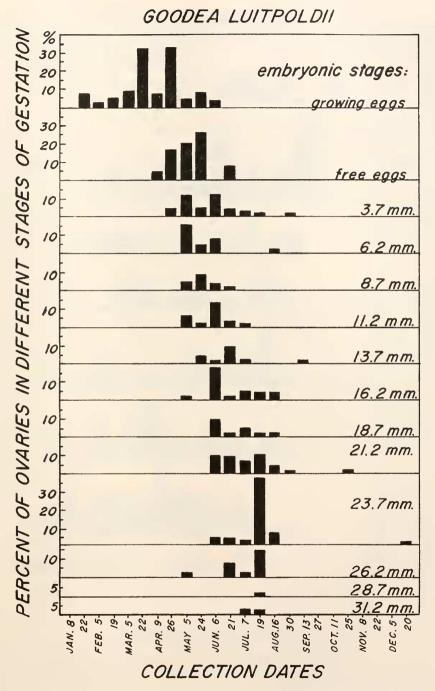


FIGURE 3. The appearance throughout the year of ovaries of *Goodea luitpoldii* with embryos in different stages of development. For any one day, the bars represent the percentage of ovaries in each stage of gestation.



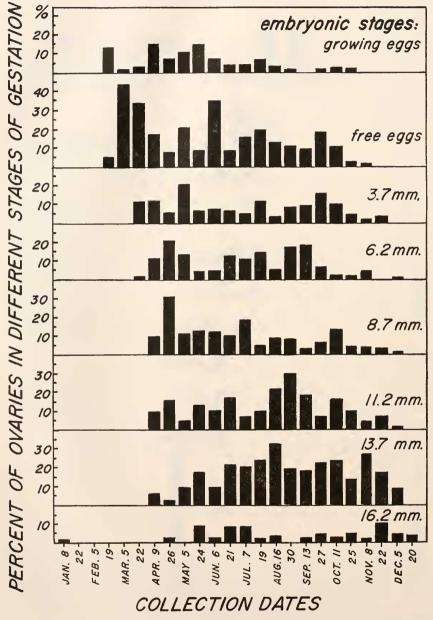


FIGURE 4. The appearance throughout the year of ovaries of *Ncoophorus diazi* with embryos in different stages of development. For any one day, the bars represent the percentage of ovaries in each stage of gestation.

to distinguish between post-partum and resting ovaries. The appearance of postpartum ovaries in *Goodea* was the same as in *Alloophorus*. In *Neoophorus*, these ovaries appeared throughout most of the year.

CHARACTERISTICS OF THE GESTATION CYCLE

Length of cycle

Estimates of the length of the gestation cycle in the three species can only be suggestive. In *Alloophorus* there was approximately a two-month period between the first appearance of free eggs (April 9) and the first appearance of post-partum ovaries (June 21). Similarly, the last collection date of free eggs was June 6 and the last appearance of embryos of maximum size was August 16, a period slightly in excess of two months. Similar calculations can be made for *Goodea* and *Neo-ophorus* from the data. From this it follows that the length of gestation is approximately 60–75 days. This admittedly is only an approximation of the length of gestation but the evidence appears sound.

Number of broods per year

The evidence is conclusive that in *Alloophorus* and *Goodca* there is but one brood per season. In *Alloophorus*, free eggs disappeared from collections even before the first young were born; hence even the females with the first broods could not start a second brood. In *Goodca*, the evidence is similar. In *Neoophorus*, the conditions are quite different. Young were born continuously between April and January; there was no good evidence of periodicity of any kind. Thus the cycle in *Neoophorus* could be a single brood with females starting at different times or the cycle could be a multiple one. If gestation takes approximately two months, these females could undergo at least three broods in one season, depending on the length of the brood interval. The fact that young are born over such a prolonged period during the year explains the difference in the curves for the immature and postpartum ovaries for *Neoophorus* (Fig. 1) as compared to the other two species.

Brood size

Estimates of brood size in the three species are based on sample counts madeduring different periods of development in the three species. In *Alloophorus* an average of 23.7 young per ovary was counted in a total of 50 ovaries containing 1186 young. In *Goodea*, there were 860 young in 44 ovaries for an average of 19.1 young. In *Neoophorus*, 193 ovaries with 7677 young gave an average of 39.9^y young per ovary.

Brood uniformity

All embryos in any one ovary are essentially of the same size. Measurements of all embryos in many ovaries indicated clearly that embryos seldom differed more than 2 to 3 mm. in total length in any one ovary. This uniformity of development is true for all three species.

Abnormal young or runts were very scarce. In *Neoophorus*, runts comprised only 0.49% of a total of 7677 sample embryos; in *Alloophorus* there were 0.42% in 1186 embryos; and in *Goodea* there were only 0.11% in 860 embryos.

Life span of females

There is a general belief among the fishermen that females normally die after reproducing. If this were true, all or most females caught early in the spring would tend to be of minimum length; collections do not support this belief. Measurements of more than 500 females in the three species indicated that fish caught in the spring showed a size range typical for females of each species. However, by using a net with finer mesh unusually small specimens were also caught; these had the following measurements: Alloophorus, 60-90 mm.; Goodea, 75-85 mm.; and Neoophorus 50 mm, or less. The commercial fishermen normally do not keep these small specimens; they form a population with a normal distribution curve at a smaller sizerange than that for normal adults. This was true for Alloophorus and Goodea. It is suggested here that these are one-year-old specimens and that they probably attain maturity during the second breeding season following the year of their birth. Plotting the lengths of all females collected shows a definite bimodal curve; the two peaks presumably represent the two populations, the one-year-old specimens and the normal adults. *Neoophorus*, on the other hand, does not show this condition. A comparable curve for this species is a single but skewed curve. It is likely that these young attain maturity during the breeding season immediately following their birth; consequently, one-year-old young merge into the size-range of the adults. In this species, overlap in size between one-year-old specimens and normal adults is due in part to the extended breeding period of this species.

Age of female and onset of reproductive activity

Making use of collections involving 513 females of the three species, information was obtained concerning the relationship between age and size of the female and brood production. There is no question that the larger females have the larger gonads; this is evident in Table I:

Size of female	Number of females	Average size of ovaries (length × diameter)
90 mm.	8	25.0×9.6 mm.
95	12	27.2×10.1
100	12	29.0×12.0
105	9	37.0×15.5
110	8	32.5×14.0
115	4	43.5×15.2
120 and over	3	43.0×19.3

The relationship between size of female and size of ovary in 56 Alloophorus females collected on May 28, 1956

TABLE I

There is a definite correlation between the diameter of an ovary and the size of the female. It should be noted that at this time of the year most females were in some stage of gestation. From these same figures it was determined that the largest young were found in the largest females. This can only mean that the largest females started their reproductive cycle earlier in the season. Except for small variations, the collections for *Goodea* and *Alloophorus* all confirmed the data given above; the May 28 collection is representative. In *Neoophorus*, how-

ever, such a progressive relationship does not exist. This can be interpreted only in the light of the extended, presumably multiple and non-rhythmic reproductive cycle of this species. Since there is no evidence of synchrony in the cycle of this species, it means that on any given day any two females of similar size can be in different stages of reproduction. Under these conditions, there can be no consistent relationship between size of female and size of developing embryos.

DISCUSSION

Both *Alloophorus* and *Goodea* have a short reproductive cycle with but one brood per year. In these two species the young were born only during a period of two months; the females were inactive during the rest of the year. It is likely, however, that *Neoophorus* has multiple broods during the breeding season, although conclusive evidence is not indicated by the data. In Neoophorus the breeding season extended over a period of 8 to 9 months of the year; this characteristic clearly distinguished *Neoophorus* from the other two species. In this respect the Neoophorus cycle approaches that of Brachyrhaphis episcopi in which breeding occurs throughout the year (Turner, 1938b). This extensive cycle is not surprising since Brachyrhaphis inhabits the area of Barro Colorado Island in the Panama Canal Zone where the tropical conditions are favorable to prolonged periods of breeding. In a sense, the multiple cycle of *Neoophorus* and the single cycles of Alloophorus and Goodea are antithetic. All forms live in the same lake (Pátzcuaro) and are subject to common physical factors. The long daylight factor at Pátzcuaro, which is in a tropical latitude, could lead to the long breeding cycle of Neoophorus but it has not had a similar effect on Alloophorus and Goodea. On the other hand, Pátzcuaro is at a high altitude (over 7000 feet) and the weather is cool to chilly even in the summer. This temperature factor could be conducive to the single broods in the two larger species but apparently has little effect on *Neoophorus*. Ecological factors in the lake could play a role, since there is some evidence of ecological segregation of species, but the lake is too shallow and probably too homogeneous to provide great ecological differences. In the final analysis, it appears that genetic differences between the three species must perforce play an important role in determining the different reproductive cycles. Among other goodeids, it is known that multiple cycles exist in *Neotoca bilineata* (Mendoza, 1939) and Xenotoca eiseni (unpublished data). Among fresh-water viviparous forms, multiple broods are common; this condition is found in forms such as Heterandria formosa (Seal, 1911; Turner, 1937); Gambusia affinis (Hildebrand, 1917; Turner, 1937); Lebistes reticulatus (Turner, 1937; Purser, 1938); Anableps anableps (Turner, 1938a) and many others. The single breeding cycle per year found in Alloophorus and Goodea is more commonly found in marine viviparous teleosts such as Zoarces viviparus (Stuhlmann, 1887; Wallace, 1903) and Cymatogaster aggregatus (Eigenmann, 1892). It has not been reported in any other goodeid.

In the three species, eggs undergo fertilization immediately before or after escape of the egg from the follicle, since all cleavage and later stages are found only in the ovarian lumen. This condition has been reported for goodeids in general (Turner, 1933), *Neotoca bilineata* (Mendoza, 1941), and it also exists in *Xenotoca eiseni* (unpublished data). Similar early evacuation of the egg from the follicle has been well established for species such as *Cymatogaster aggregatus* (Eigenmann, 1892; Turner, 1947), Jenynsia lineata (Scott, 1928; Turner, 1940b) and others. This condition stands in direct contrast to that found in Anableps anableps (Turner, 1938a) and poeciliids in general (Turner, 1947), for fertilization and most or all development takes place in a follicle within the ovarian tissues. The young escape from the follicle only shortly before birth.

Insemination and fertilization occur in rapid succession in the three goodeid species, each brood requiring a separate insemination. Sperm have been observed in the ovaries only about time of fertilization. Although breeding occurs only over a short period of time in the two species, the males of all three species show abundant sperm in the testes during the entire year. In *Neotoca bilineata* (Mendoza, 1941) each of the multiple broods also requires a separate insemination. Furthermore, the phenomenon of sperm storage within the female genital tract does not occur in any goodeid. Stored sperm are believed to permit fertilization of successive broods without necessity for further contact between nule and female. The phenomenon of sperm storage and successive fertilization of two or more broods without need for separate inseminations has been described for many viviparous teleosts, such as *Jenynsia lineata* (Scott, 1928; Turner, 1957), *Cymatogaster aggregatus* (Eigenmann, 1892), *Gambusia affinis* (Hildebrand, 1917), *Xiphophorus helleri* (van Oordt, 1928) and others.

Another phenomenon which is absent in goodeids but is very common in poeciliids is the phenomenon of superfetation, a condition in which two or more broods at different stages of development occupy an ovary at the same time. Examples among poeciliids that demonstrate an extreme form of superfetation are Autophallus and Poeciliopsis (Turner, 1937), in which as many as nine overlapping broods occur at one time; other poeciliids show varying degrees of superfetation. Failure to achieve superfetation among goodeids is due, in part, to the failure of eggs to grow to maximum size before expulsion of a brood and, in part, to the absence of sperm storage. These two conditions normally occur in many poeciliids and are requisites for the occurrence of superfetation. In contrast to the writer's observations, Turner (1940a) states that he has seen aberrant or unsuccessful examples of superfetation in goodeids such as Xenoophorus erro, Chapalichthys en*caustus, Skiffia variegata* and others, because he has seen sperm and growing oocytes in the ovaries, superimposed on another brood. The possibility certainly exists that occasional eggs may grow, be fertilized, and start development during gestation. In the goodeids studied by the writer, all abnormal embryos observed were so scarce and so close to the stage of development of the current brood that they were all interpreted as abnormalities rather than as younger embryos superimposed on the normal brood.

In Alloophorus and Goodea, broods average around 20 young but fluctuate under 50. In contrast, broods in Neoophorus average about 40 young but may on occasion exceed 100. These brood sizes compare favorably with those in Xenotoca eiseni (unpublished data); Neotoca bilineata (Mendoza, 1939) has much smaller broods, averaging only six to ten young. Broods numbering under 50 young are very common among viviparous fresh-water fishes. For example, Gambusia affinis (Kuntz, 1913) has 40 to 63 young per brood, Jenynsia lineata (Scott, 1928) has 10 to 40 young, and there are 30 to 40 young per brood in Xiphophorus maculatus (formerly Platypoecilus maculatus) (Tavolga and Rugh, 1947; Tavolga, 1949), etc. In the goodeids studied, the larger and older females have larger broods and, although younger females do have smaller broods, the difference in brood size is not great. This condition is also true in *Neotoca bilineata* (Mendoza, 1939) and *Xenotoca eiseni* (unpublished data) although in these two forms the size of broods in the younger females is markedly smaller. This discrepancy of brood size between younger and older females is very common among other viviparous teleosts, such as *Cymatogaster aggregatus* (Eigenmann, 1892), *Gambusia affinis* (Hildebrand, 1917) *Anableps anableps* (Turner, 1938a) and others.

The occurrence of much uniformity of development among the young in any one ovary is not surprising since this is a common phenomenon. Specific reference to this condition has been reported for viviparous teleosts, such as *Neotoca bilineata* (Mendoza 1941), *Xiphophorus helleri* (Weyenbergh, 1875), *Cymatogaster aggregatus* (Eigenmann, 1892), *Mollienisia latipinna* (Turner, 1937), *Anableps anableps* (Turner, 1938a) and others.

Another impressive factor was the occurrence of very few abnormal embryos during embryonic development. It is likely that if fertilization is successful, the majority of the embryos will continue through development. Reason for this belief rests on the fact that the free egg counts for both *Alloophorus* and *Goodea* agreed well with the average size of broods. In *Neoophorus*, however, there is a greater disparity between the number of free eggs and the number of young in a brood. Even in this species, however, once the embryos start development mortality appears to be very low. The writer's observations do not agree with Turner's generalization that in the Jenynsiidae and Goodeidae many more eggs are fertilized than survive till birth (Turner, 1938a). It is important to note that Turner's observations were not based on the three species in this study.

Finally, the assumption that Alloophorus and Goodea take two years to mature appears to be unusual among viviparous teleosts. Zoarces viviparus (Wallace, 1903) is one of the few described as maturing at the end of the second year. Species such as Cymatogaster aggregatus (Eigenmann, 1892) and Jenynsia lineata (Turner, 1940b) are said to mature by the following season. It is suspected but cannot be proven that Neoophorus diazi matures by the following year. In other goodeids, such as Neotoca bilineata (Mendoza, 1939), the young mature within the same breeding season. The length of time necessary for maturation probably is related to sheer physical size of adults, along with pertinent ecological and physiological factors, since Alloophorus and Goodea are larger than typical poeciliids and apparently resemble Zoarces viviparus, another large species (130–300 mm.), in taking two years to mature.

Although some factors in the reproductive cycles of these three species have been demonstrated clearly by the collection of field specimens, it is also evident that some properties of the cycles, such as the actual length of gestation and the single or multiple nature of the *Neoophorus* reproduction cycle, will have to be determined either by tagged specimens in the field or by a laboratory-controlled study.

SUMMARY

1. The reproductive cycles were determined for three goodeids: *Alloophorus robustus, Goodea luitpoldii,* and *Neoophorus diazi*. The study is based on a year-long series of collections in the field; over 3000 females were examined.

2. Alloophorus and Goodea are shown to have a single cycle; young are born from June through August. Neoophorus probably has a multiple cycle and young are born continuously from April through January or February of the next year.

3. Brood size varies as follows: there are approximately 20 embryos per brood in both Goodea and Alloophorus but the average is about 40 in Neoophorus. Younger females have smaller broods although the difference is small.

4. Eggs are discharged from the follicle about time of fertilization and undergo all development within the ovarian lumen. On birth, young are able to swim actively.

5. There is no evidence of sperm storage or superfetation.

6. Embryos in any one brood exhibit much uniformity of size.

7. Abnormal development of embryos is at a minimum; runts constituted less than 1% of all embryos examined.

8. Neoophorus is believed to mature in one year whereas Alloophorus and Goodea are thought to take two years to develop to sexual maturity.

9. Major differences in the reproductive cycle between the three goodeids are believed to be primarily genetic in character.

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